Radiation Biology and Inherited Sterility in False Codling Moth (Lepidoptera: Tortricidae)

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ABSTRACT   False codling moth, *Cryptophlebia leucotreta* (Meyrick), male and female mature pupae and newly emerged adults were treated with increasing doses of gamma radiation and either inbred or out-crossed with fertile counterparts. For newly emerged adults, there was no significant relationship between dose of radiation and insect fecundity when untreated females were mated to treated males (N♀ by T♂). However, fecundity of treated females mated to either untreated (T♀ by N♂) or treated males (T♀ by T♂) declined as the dose of radiation increased. A similar trend was observed when mature pupae were treated. The dose at which 100% sterility was achieved in treated females mated to untreated males (T♀ by N♂) for both adults and pupae was 200 Gy. In contrast, newly emerged adult males treated with 350 Gy still had a residual fertility of 5.2% when mated to untreated females, and newly emerged adult males that were treated as pupae had a residual fertility of 3.3%. Inherited effects resulting from irradiation of parental (P_1) males with selected doses of radiation were recorded for the F_1 generation. Decreased F_1 fecundity and fertility, increased F_1 mortality during development, and a significant shift in the F_1 sex ratio in favor of males was observed when increasing doses of radiation were applied to the P_1 males.

KEY WORDS   *Cryptophlebia leucotreta*, sterile insect technique, gamma radiation, fecundity, fertility

FALSE CODLING MOTH (FCM), *Cryptophlebia leucotreta* (Lepidoptera: Tortricidae), is indigenous to southern Africa, the Ethiopian region, and many islands on the African continent (Stofberg 1954, Catling and Aschenborn 1974, Commonwealth Institute of Biological Control 1984). FCM has a wide range of host plants and has adapted to cultivated crops from its original indigenous host plants. Of the cultivated crops, it prefers citrus, but it also attacks many different deciduous, subtropical, and tropical plants (Economides 1979). It is the key pest of almost all citrus varieties in South Africa (Stofberg 1954) and is a serious pest of cotton and maize in tropical Africa (Angelini and Labonne 1970, Reed 1974). Other recorded hosts include okra, jute, pineapple, sour-sop, custard-apple, carambola, Sodom apple, tea, pepper, coffee, cola nuts, rooibos, persimmon, Surinam cherry, wild fig, mangosteen, guava, pomegranate, cacao, plum, peach, avocado, bean, lima bean, sorghum, cowpea, apricot, banana, olive, mango, litchi, English walnut, and many other indigenous African plants (Gunn 1921, Hill 1983, Pinhey 1975, Reed 1974, Staeubli 1976, Willers 1979).

In South Africa, FCM has four to six overlapping generations per year (Stofberg 1954, Georgala 1969). Females typically lay 100–250 individual eggs on fruit or foliage (Catling and Aschenborn 1974, Daiber 1978), and young larvae penetrate the fruit, where larval development is completed. Mature larvae leave the fruit and spin cocoons in the soil or in bark crevasses (Stofberg 1954, Georgala 1969). Infestation by FCM generally causes the fruit to drop before harvest (Georgala 1969). However, because larval entries take a few days to become visible, those that occur near fruit harvest are often not detected by packing house fruit graders and infested fruit can be inadvertently packaged for export (Georgala 1969).

FCM is currently not present in the United States. Many U.S. Federal and State Agencies have expressed concern that this pest could soon be introduced into the United States as a direct result of increased international trade and tourism between the United States and many African countries. USDA-APHIS Port Interception Network records indicate that these concerns are well founded. Since 1985, FCM has been intercepted 122 times at 19 different U.S. ports of entry. The interceptions were detected in 22 different host plants originating in 15 different African countries. Because FCM infests so many different host plants and because it would be a quarantine issue for some important commodities, establishment of this pest in the United States could result in economic losses in the billions of dollars.

In South Africa, FCM has documented resistance to benzyl-ureas (Hofmeyr and Pringle 1998) that are commonly used for its control. Other suppression strategies, such as orchard sanitation and the use of

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pathogens, predators, and parasitoids have had limited success and cannot be used as stand-alone tactics (Newton 1998). A sex pheromone has been identified for FCM (Read et al. 1968, 1974, Henderson and Warren 1970, Parsoons et al. 1976, Hofmeyr and Calitz 1991); however, mating disruption is not used for population suppression. Currently, an augmentative biological control program using the egg parasitoid *Trichogrammatoidea cryptophlebiae* Nagaraja (Hymenoptera: Trichogrammatidae) is underway in South Africa (Newton 1988, 1989, Newton and Odendaal 1990). The parasitoids are mass-reared on eggs of FCM, and production per month is sufficient to treat 600–800 ha of commercial citrus. However, augmentative releases of *T. cryptophlebiae* alone cannot invariably realize the level of control needed in citrus and pesticide applications continue to be required.

We propose to develop a sterile insect technique (SIT) program for FCM that could be used as an area-wide pest management tactic in South Africa and as an eradication tool if FCM is introduced into the United States. As with other SIT programs, the ability to mass rear and sterilize the insects are necessary first steps in developing this technology. Fortunately, mass rearing of FCM is already underway in South Africa to generate host eggs for mass rearing of *T. cryptophlebiae* egg parasitoids. Mass rearing of FCM was originally described by Ripley et al. (1939) and modified by Theron (1947) and Schwartz (1972). Furthermore, Myburgh (1963), Schwartz (1978), and Du Toit (1981) conducted preliminary studies on the radiation biology of FCM in South Africa. However, these authors did not document the effect of mating treated males with treated females (T♀ by T♂), investigate the possibility of irradiating adults rather than pupae, or document the presence of inherited sterility (North 1975, LaChance 1985) in the first filial generation of FCM.

Herein we report on the effect of increasing doses of gamma radiation on the fecundity and fertility of FCM when insects were inbred or out-crossed to untreated (fertile) mates. We determined the minimum dose at which treated females were 100% sterile when mated to untreated (fertile) males. Based on the results of the first set of experiments on the parental (P_1) generation, three doses were chosen for documentation of inherited sterility effects in the F_1 generation of FCM. Mortality during development, sex ratio distortion, and fecundity and fertility of the F_1 generation produced from treated (P_1) males and untreated females are presented herein. The minimum dose at which irradiated (P_1) males produce 100% sterile offspring is reported. The results obtained are discussed in the context of their applicability in the development of an SIT program against FCM for use in South Africa and in the United States, and the possible combination of the SIT program with augmentative releases of the egg parasitoid *T. cryptophlebiae* to bring about synergistic pest suppression as suggested by the mathematical models of Knipling (1992) and Carpenter (1993, 2000).

Materials and Methods

Test Insects and Artificial Diet. FCM used in these experiments were provided by Cederberg Biocontrol Systems, Citrusdal, South Africa. The colony has been in continuous culture since 1978 ($\approx$10 generations/ yr). Insects are reared on an autoclaved maize meal paste inoculated with *Rhizopus* sp. as described by Ripley et al. (1939) and modified by Theron (1947). FCM are reared so that eggs can serve as host material for commercial production of the parasitoid *T. cryptophlebiae* (Hymenoptera: Trichogrammatidae).

Effect of Gamma Radiation on Adult Moth Sterility—Adults Treated. Experiments were conducted in June 2002 at the INFRUITEC laboratories in Stellenbosch, South Africa. FCM pupae were removed from their cocoons, sorted by sex, placed in aluminum screen cages (30 by 30 by 30 cm), and allowed to emerge at 26 ± 1°C, 10:14 (L:D) photoperiod, and 65–70% RH. Cohorts of five virgin adult FCM males and females (<24 h old) were chilled (0–2°C) and exposed to gamma radiation. The irradiator was a panoramic Cobalt-60 point source (currently $\approx$6,000 Curie) centrally located in a turntable 1 m in diameter. Treatment samples were placed on one or more of eight smaller turntables, each 200 mm in diameter and situated equidistant on the periphery of the main turntable. The smaller turntables counter rotated to enable 360° treatment of the treatment samples. Dose rates measured in sample positions were verified with each exposure and decreased from 8.47 to 7.54 Gy/min (±<5%, Fricke dosimetry) during the course of the study. The FCM were treated with doses of 0, 50, 100, 150, 200, 250, 300, and 350 Gy.

After irradiation, treated moths were placed inside triangular waxed-paper oviposition cages (20 by 14 by 15 cm) with equal numbers of treated (T) or untreated (N) adults of the opposite sex ($n = 10$/cage, 5 ♀ and 5 ♂). The insects were allowed to mate and lay eggs at the abovementioned conditions for 6 d, after which the moths were killed by freezing, and all females from each treatment were dissected to determine their mating status (spermatophores present in the bursa copulatrix) (Ferro and Akre 1975). Paper cages with eggs were incubated for 5 d at the same conditions to allow for complete egg development and larval eclosion. The total number of eggs laid (fecundity) and the number of eggs that hatched (fertility) were counted per cage at each dose. Sterility was expressed as the percentage of eggs that failed to hatch. Three types of crosses were made at each dose (T♀ by N♂, N♀ by T♂, and T♀ by T♂), and five replicates of each cross at each dose were completed.

Effect of Gamma Radiation on Moth Sterility—Mature Pupae Treated. Procedures were the same as above with the following exceptions. Pupae were sorted by sex, placed in 16-oz plastic containers, and allowed to mature until pharate adults were visible through the pupal integument. Mature male and female pupae (<24 h from adult emergence) were exposed to gamma radiation at the doses indicated above and returned to the laboratory, and adults were al-

lowed to eclose in the plastic containers. Cohorts of five virgin adult males and females (<24 h old) were placed in oviposition cages as above. Two types of crosses (T♀ by N♂ and N♀ by T♂) and three replicates of each cross at each dose were completed.

Documentation of F_1 Inherited Effects. Experiments were conducted in September and October 2002 at the Citrus Research International and IN-FRUITEC laboratories in Citrusdal and Stellenbosch, South Africa, respectively. Based on results obtained in the previous experiments, cohorts of five virgin adult FCM males (<24 h old) were either left untreated or were irradiated at 100, 150, 200, and 250 Gy. Males from each treatment were placed in waxed paper oviposition cages with equal numbers of untreated females of the same age (parental [P_1] generation; $n = 10$/cage, 5 ♀ and 5 ♂). A variable number of replicates at each dose were set up to account for differences in fecundity and fertility (the higher the dose of radiation applied to the ♂, the lower the fecundity and fertility when mated to an untreated ♀). The number of replicates ranged between 8 and 25 depending on the radiation dose given to the male parent. Moths were allowed to mate and lay eggs at 26 ± 1°C, photoperiod of 14:10 (L:D), and 65–70% RH for 4 d. Insects were killed by freezing, and all females were dissected to ascertain their mating status. Sections of egg sheet from each treatment were cut to fit inside the glass rearing bottles. The total number of eggs per egg sheet section were counted and sections were placed inside bottles with freshly prepared FCM diet. Bottles containing F_1 eggs were kept at 26 ± 1°C, photoperiod of 14:10 (L:D), and 65–70% RH for 7 d, at which time egg sheet sections were removed from the bottles. The total number of eggs that hatched per treatment was recorded. Sterility at each dose was expressed as the percentage of eggs that failed to hatch.

Surviving larvae (F_1 progeny) were allowed to continue developing in the diet bottles at the abovementioned conditions for 4 wk. Normal cotton wool stoppers were replaced with C-flute corrugated cardboard stoppers after ≈3 wk to aid in the collection of pupae. When pupation was complete, the total number and the gender of live pupae in the stoppers and in the larval diet were recorded per bottle at each dose. F_1 mortality (during rearing) was obtained by subtracting the number of live pupae from the number of eggs that hatched per treatment. The F_1 pupae were placed in individual vials for adult emergence; kept at 26 ± 1°C, photoperiod of 14:10 (L:D), and 65–70% RH; and used to determine the presence of F_1 sterility in the next experiment.

Determination of FCM F_1 Sterility. Approximately 1,000 untreated pupae were collected from rearing bottles, placed in individual vials, and kept at the above conditions until emergence to serve as mates for the emerging F_1 material. Emerging male and female F_1 adults (<24 h old) from the previous experiment were individually paired with untreated adults of the opposite sex inside small stainless steel mesh cages (2.5 cm high by 6 cm diameter) placed on top of waxed paper egg sheets. The date of initial pairing was recorded. Ten replicates were set up for each cross at each dose as follows:

Dose (Gy)	F_1♀ × N♂	N♀ × F_1♂	F_1♀ × F_1♂	N♀ × N♂
0 (control)	—	—	10	10
100	10	10	10	—
150	10	10	10	—
200	10	10	10	—
250	10	10	10	—

The moths were allowed to mate and lay eggs for 7 d. Insects were killed by freezing, and all females were dissected to ascertain their mating status. Egg sheets were incubated for 5 d at the above conditions to allow for complete egg development and larval eclosion. The total number of eggs laid and the number of eggs that hatched were counted per cross at each dose. Sterility was expressed as the percentage of eggs that failed to hatch.

Statistical Analysis. Data collected from the parental (irradiated) generation for both newly emerged adults and mature pupae were analyzed using a three-factor analysis of variance (ANOVA) and regression analysis, with dose used, stage irradiated, and parental cross as sources of variation (PROC ANOVA and PROC GLM) (SAS Institute 1989). Because there was a significant ($P \leq 0.05$) interaction between dose and stage irradiated, the effect of dose within each stage irradiated was examined in separate two-factor analyses. Dose used was the independent variable and the percentage egg hatch (arcsine transformed) and number of eggs laid were the dependent variables. When significant ($P \leq 0.05$) interactions were detected between dose used and parental cross, the effect of dose within each cross was examined using polynomial regression.

The effect of radiation dose on developmental time (date of egg placement on diet until adult emergence) of the F_1 progeny of irradiated males crossed with normal females was examined using polynomial regression. Data on the percentage of F_1 neonates surviving to adulthood and the sex ratio (percentage male) of F_1 adults were transformed (arcsine) and analyzed using ANOVA and regression analysis, with dose of radiation as the source of variation (PROC ANOVA and PROC GLM) (SAS Institute 1989).

Data collected for the F_1 adult generation were analyzed using a two-factor ANOVA and regression analysis, with dose and F_1 cross as sources of variation (PROC ANOVA and PROC GLM) (SAS Institute 1989). Dose used was the independent variable, and the percentage egg hatch (arcsine transformed) and number of eggs laid were the dependent variables. When significant ($P \leq 0.05$) interaction was detected between dose used and cross, the effect of dose within each cross was examined using polynomial regression.
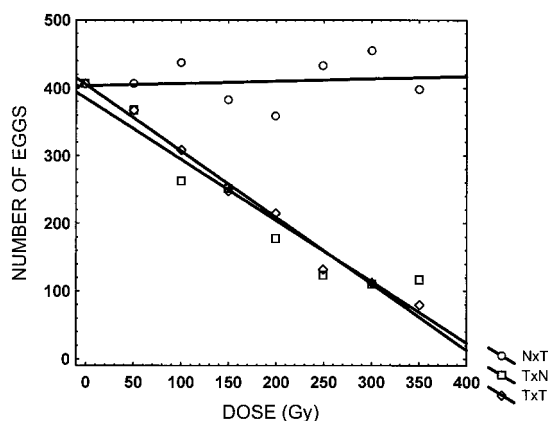
Fig. 1. Effect of dose of radiation administered to *C. leucotreta* adults on the fecundity (mean number of eggs laid) per mated female. Males and females were treated (T) with 0, 50, 100, 150, 200, 250, 300, and 350 Gy and inbred (T♀ by T♂) or out-crossed (T♀ by N♂, N♀ by T♂) to normal (N, untreated) adults. Regression equations are given in text.

Results

Effect of Gamma Radiation on Moth Sterility—Adults and Mature Pupae. The fecundity (total number of eggs) of newly emerged adults was affected by the dose of radiation and by the gender irradiated, resulting in a significant ($F = 4.63$; df = 14, 128; $P < 0.0001$) interaction between dose and parental cross (Fig. 1). In the cross where only the male was irradiated (N♀ by T♂), there was no significant relationship between dose of radiation and insect fecundity. However, parental crosses involving irradiated females produced significantly (T♀ by N♂; $y = 408.4 - 0.98x$; $F = 167.1$; df = 1, 36; $P < 0.0001$) (T♀ by T♂; $y = 407.4 - 0.74x$; $F = 117.2$; df = 1, 36; $P < 0.0001$) fewer eggs as the dose of radiation increased (i.e., from
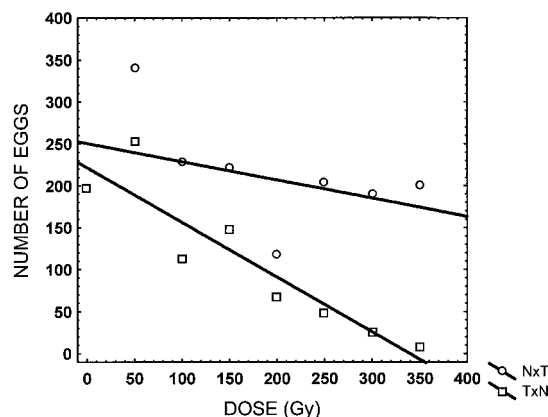

Fig. 2. Effect of radiation dose administered to *C. leucotreta* pupae 24 h before adult eclosion on the fecundity (mean number of eggs laid) per mated female. Males and females were treated (T) with 0, 50, 100, 150, 200, 250, 300, and 350 Gy and out-crossed (T♀ by N♂, N♀ by T♂) to normal (N, untreated) adults. Regression equations are given in text.
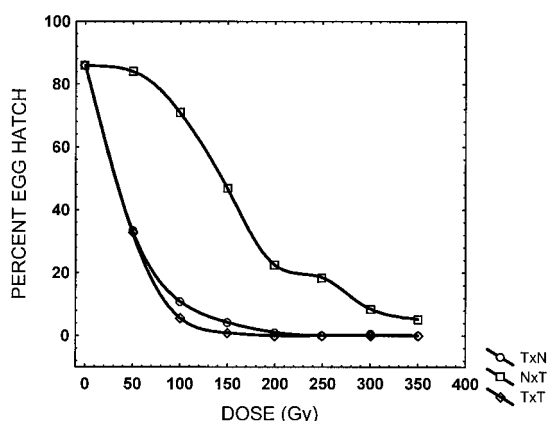

Fig. 3. Effect of radiation dose administered to *C. leucotreta* adults on the fertility (mean percentage of eggs that hatched) per mated female. Males and females were treated (T) with 0, 50, 100, 150, 200, 250, 300, and 350 Gy and inbred (T♀ by T♂) or out-crossed (T♀ by N♂, N♀ by T♂) to normal (N, untreated) adults. Regression equations are given in text.

400 eggs per female at 0 Gy to circa 100 eggs per female at 350 Gy). A similar trend was observed for irradiated pupae (Fig. 2). Only crosses involving irradiated females produced significantly (T♀ by N♂; $y = 213.6 - 0.05x$; $F = 25.2$; df = 1, 20; $P < 0.0001$) fewer eggs as the dose of radiation applied to the females increased.

The percentage of eggs that hatched (percentage fertility) from irradiated newly emerged adults was significantly affected by the gender irradiated and by the dose of radiation used. For each gender, the percentage of eggs that hatched declined significantly as the dose of radiation increased (Fig. 3). This dose effect was greater for crosses involving irradiated females (T♀ by N♂; $y = 83.7 - 1.16x + 0.005x^2$; $F = 232.13$; df = 1, 36; $P < 0.0001$; T♀ by T♂; $y = 84.3 - 1.25x + 0.006x^2$; $F = 330.87$; df = 1, 36; $P < 0.0001$) than it was for crosses involving irradiated males (N♀ by T♂; $y = 87.8 - 0.015x - 0.002x^2$; $F = 26.85$; df = 1, 36; $P < 0.0001$). Irradiated females were almost completely sterile at a dose of 200 Gy, while irradiated males had a residual fertility of 5.2% at a dose of 350 Gy. The percentage of eggs that hatched also declined significantly as the dose of radiation increased when mature pupae were treated (Fig. 4). Again, this dose effect was greater for irradiated females (T♀ by N♂; $y = 88.5 - 1.346x + 0.006x^2$; $F = 194.44$; df = 1, 20; $P < 0.0001$) than for irradiated males (N♀ by T♂; $y = 89.5 - 0.218x$; $F = 26.85$; df = 1, 20; $P < 0.0001$). Irradiated female pupae were completely sterile at a dose of 200 Gy, but irradiated male pupae had a residual fertility of 3.3% at a dose of 350 Gy. One hundred percent of the females in both (adult and mature pupae) irradiation experiments were mated.

Documentation of F$_1$ Inherited Effects. The percentage of F$_1$ neonates (from crosses of N♀ by T♂) that survived to adulthood was inversely related ($y = 55.86 - 0.13x$; $F = 26.76$; df = 1, 11; $P < 0.0001$) to the dose of radiation given to the male (P$_1$) parent (Fig.
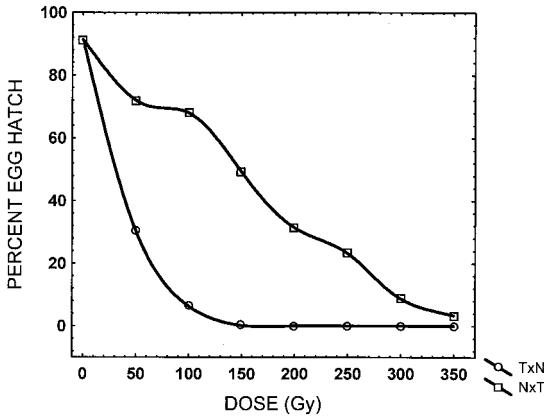
Fig. 4. Effect of radiation dose administered to *C. leucotreta* pupae 24 h before adult eclosion on the fertility (mean percentage of eggs that hatched) per mated female. Males and females were treated (T) with 0, 50, 100, 150, 200, 250, 300, and 350 Gy and out-crossed (T♀ by N♂, N♀ by T♂) to normal (N, untreated) adults. Regression equations are given in text.

Fig. 6. Relationship between the dose of radiation administered to *C. leucotreta* adult P_1 males and the mean number of days required for F_1 neonates to develop into adults. Males were treated with 0, 50, 100, 150, 200, and 250 Gy and out-crossed to normal females (N♀ by T♂). Regression equation is given in text.

5). A similar relationship was observed when we analyzed the percentage of F_1 eggs that survived to adulthood. In addition to increasing the rate of mortality in the F_1 generation, the dose of radiation given to the male parent significantly ($y = 15.42 + 0.02x$; $F = 56.66$; df $= 1, 13$; $P < 0.0001$) increased the mean number of days required for larval development and emergence of the F_1 adult (Fig. 6). The mean number of days required for larval development and adult emergence in untreated FCM was 15–16 d, while in F_1 FCM developing from crosses where the male parent received 250 Gy, larval development and adult emergence took 20–22 d. Furthermore, the sex ratio of the F_1 adults was significantly ($y = 45.04 + 0.13x$; $F = 86.10$; df $= 1, 11$; $P < 0.0001$) affected by the dose of
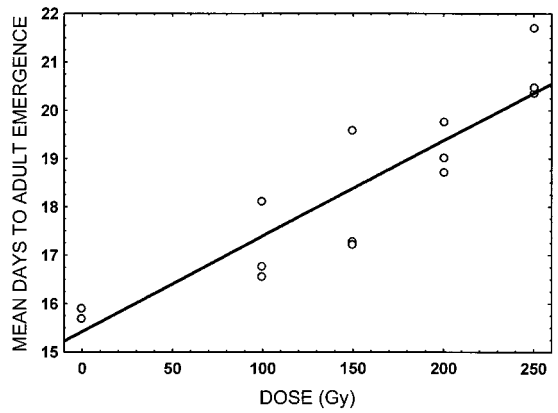
radiation given to the male parent (Fig. 7). The percentage of male F_1 adults increased as the dose of radiation increased to reach almost 100% males at 250 Gy.

Determination of FCM F_1 Sterility. The fecundity (total number of eggs) of F_1 adults outcrossed to untreated counterparts was affected by the dose of radiation given to the male (P_1) parent and by the type of F_1 cross, resulting in a significant ($F = 4.11$; df $= 8$, 125; $P = 0.0002$) interaction between dose and cross (Fig. 8). In crosses where F_1 females were mated to untreated males (F_1♀ by N♂), there was a significant ($y = 592.1 - 3.54x$; $F = 22.2$; df $= 1, 44$; $P < 0.0001$) linear relationship between dose of radiation given to her father and the fecundity of the (F_1) cross. However, in crosses involving F_1 males (N♀ by F_1♂ and F_1♀ by F_1♂), there were significant quadratic rela-
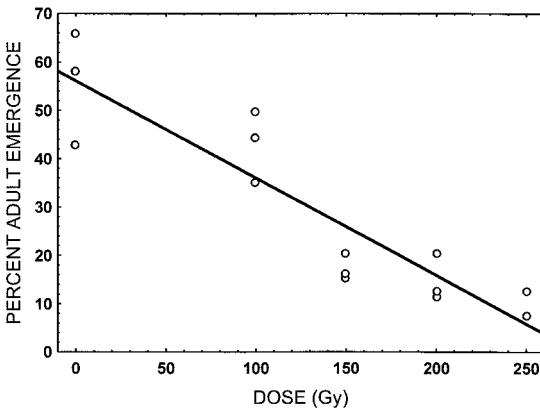

Fig. 5. Relationship between the dose of radiation administered to *C. leucotreta* adult P_1 males and the mean percentage of F_1 neonates that developed into adults. Males were treated with 0, 50, 100, 150, 200, and 250 Gy and outcrossed to normal females (N♀ by T♂). Regression equation is given in text.
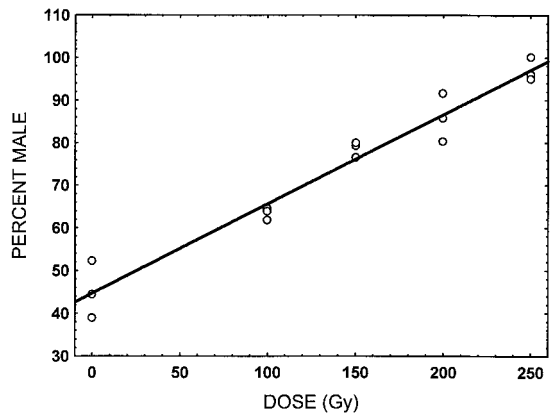

Fig. 7. Relationship between the dose of radiation administered to *C. leucotreta* adult P_1 males and the mean percentage of F_1 adults that were male. Males were treated with 0, 50, 100, 150, 200, and 250 Gy and out-crossed to normal females (N♀ by T♂). Regression equation is given in text.
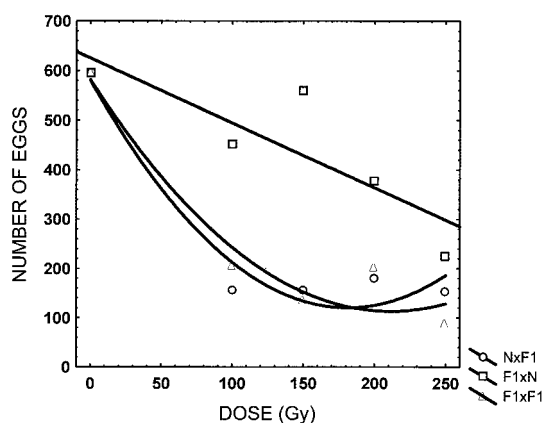
Fig. 8. Effect of radiation dose administered to *C. leucotreta* adult P_1 males on the fecundity (mean number of eggs laid) in the F_1 generation per mated female. Males were treated with 0, 50, 100, 150, 200, and 250 Gy and inbred to normal females (N♀ by T♂). F_1 progeny from these crosses were inbred (F_1♀ by F_1♂) and out-crossed (F_1♀ by N♂, N♀ by F_1♂) to normal (N, untreated) moths. Regression equations are given in text.
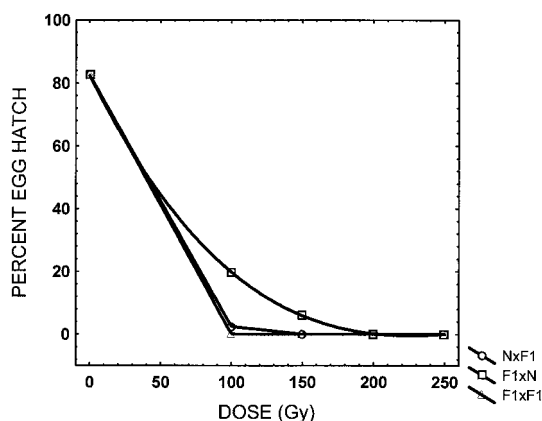

Fig. 9. Effect of radiation dose administered to *C. leucotreta* adult P_1 males on the fertility (mean percentage of eggs that hatched) in the F_1 generation per mated female. Males were treated with 0, 50, 100, 150, 200, and 250 Gy and inbred to normal females (N♀ by T♂). F_1 progeny from these crosses were inbred (F_1♀ by F_1♂) and out-crossed (F_1♀ by N♂, N♀ by F_1♂) to normal (N, untreated) moths. Regression equations are given in text.

tionships between dose of radiation and insect fecundity, resulting in fewer eggs being produced as the dose of radiation increased (N♀ by F_1♂; $y = 595.2 - 9.0x + 0.058x^2$; $F = 28.7$; df = 1, 44; $P < 0.0001$; F_1♀ by F_1♂; $y = 597 - 8.37x + 0.054x^2$; $F = 27.45$; df = 1, 40; $P < 0.0001$). The percentage of eggs that hatched (percentage fertility) from F_1 adults also was affected by the dose of radiation given to the male parent and by the F_1 cross, again resulting in a significant ($F = 5.11$; df = 8, 122; $P = 0.0001$) interaction between dose and cross (Fig. 9). F_1 females crossed with normal males (N♂) had greater residual fertility than did normal (N♀) or F_1 females crossed with F_1 males. The F_1 males crossed with untreated females (N♀) were 100% sterile when their father had been treated with a dose of 150 Gy.

Discussion

LaChance (1985) described several attributes commonly reported from studies on inherited sterility in different species of Lepidoptera. These attributes include differential sensitivity to radiation between males and females in the parental (P_1) generation, F_1 male and female offspring that are more sterile than the irradiated P_1 generation, more male progeny than female progeny produced in the F_1 generation, longer developmental time in the F_1 generation, and reduced sperm quality in the F_1 generation. The data obtained for FCM are congruent with data from previous studies on inherited sterility in other Lepidoptera, particularly with the results reported by Bloem et al. (1999) for the codling moth, *Cydia pomonella*, which belongs to the same family as FCM—the family Tortricidae. In general, FCM was more resistant to radiation than codling moth, and the sex ratio distortions evident in the F_1 generation were more pronounced for FCM.

However, both species responded similarly to increasing doses of radiation with respect to decline in insect fecundity and rise in insect sterility in both the parental and F_1 generations and in the developmental delay experienced in the F_1 generation.

Selection of the most appropriate dose of radiation with which to treat pest insects is a critical element in developing an SIT program. The importance of dose selection increases when no practical method is available to separate the insects by gender *en masse*, requiring both males and females to be irradiated and released into the environment as is currently the case in all SIT programs against Lepidoptera (Stewart 1984, Bloem and Bloem 2000). While it is crucial that released females be sufficiently sterile to avoid increasing host plant damage caused by the production of (sterile) F_1 larvae, it is also crucial that the dose of sterilizing radiation be kept as low as possible to maintain mating competitiveness, particularly because Lepidoptera are relatively radio-resistant compared with other insects. Fortunately, because female Lepidoptera are generally sterilized at lower doses of radiation than are males and because partially sterilized males produce F_1 progeny with increased levels of sterility, a treatment dose can usually be selected at which the released females are 100% sterile and the released males produce only a limited number of F_1 progeny that are predominantly male and 100% sterile when mated with feral females. The dose of radiation providing these valuable attributes in FCM was found to be 150–200 Gy.

Two potential SIT programs are under investigation for the FCM in South Africa—releases of irradiated FCM alone and releases of irradiated FCM combined with *T. cryptophlebiae.* The objective in both cases would be to provide an economical, sustainable and environmentally friendly method of control for FCM

in citrus. In the case of a combined SIT + biological control approach, the synergism between tactics predicted by mathematical models published by Knipling (1992) and Carpenter (1993, 2000) would hopefully bring about pest suppression more quickly. An increased number of eggs laid by irradiated and released FCM may provide additional host material for *T. cryptophlebiae* and thereby increase the number of parasitoids that would be available in subsequent generations. Eggs from irradiated FCM that are not used as host material by *T. cryptophlebiae* would either fail to hatch (T♀ by N♂, T♀ by T♂) or would hatch (N♀ by T♂) and develop into sterile F_1 adults that would provide additional pest population suppression. However, additional research needs to be conducted before recommending this approach to South African citrus growers. In countries where FCM does not occur (e.g., the United States), the technologies and methodologies for an SIT program against FCM developed for South Africa could be available for use in an eradication campaign should the FCM become established as an exotic invasive pest. In all of these scenarios, the release of completely sterile females and partially sterile males (able to produce sterile F_1 progeny when mating with feral females) likely would be the most appropriate strategy. The results from this study provide a foundation of knowledge to advance the development of these SIT strategies. Currently, we are investigating the competitiveness of irradiated FCM and examining the compatibility of the SIT for FCM with augmentative releases of *T. cryptophlebiae.*

Acknowledgments

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